*THE LACERTID EAR: EREMIAS ARGUS**

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The inner ear structure of members of the lizard family Lacertidae is unusual in that there are two basilar membranes lying end to end, stretched over separate oval-shaped openings in the limbic plate. The separation between the two openings is a narrow isthmus of the same peculiar, dense connective tissue that constitutes the main frame.

Whether every member of this family exhibits this peculiarity remains to be determined, for the ears of only a few of the numerous species belonging to this group have been studied. The first observations of this dual structure seem to be those of Deiters,[1] in 1862, who described and pictured the inner ear of *Lacerta agilis*. Clason,[2] in 1873, repeated the observations on *Lacerta agilis* and perhaps extended them to *Lacerta ocellata* (of which he had a single specimen). These investigators were evidently unaware of the unusual character of the lacertid ear, for they did not examine representatives of other lizard families and seem to have assumed that the condition found in their specimens was typical.

However, Retzius,[3] in 1884, knew about the peculiar structure of the lacertid ear. He studied 11 species of lizards, of which 2 were lacertids—*Lacerta viridis* and *Lacerta ocellata*—and in both he found two separate basilar membranes. He reported a similar duplex structure in *Psammosaurus caspius*, a varanid. The remaining eight species had single basilar membranes.

Miller,[4] in 1966, in his broad survey of the gross structure of the cochlear duct of lizards, listed nine species of lacertids (belonging to five genera) in which this duality of structure was found. These species were *Acanthodactylus cantoris, Eremias argus, Eremias guttulata, Lacerta dugesii, Lacerta viridis, Lacerta vivipara, Psammodromus argirus, Psammodromus hispanicus,* and *Tachydromus septentrionalis*.

The structure of the lacertid ear has been studied in detail in only one species, *Eremias velox persica*.[5] The observations on this form revealed not only that two basilar membranes are present but also that there are significant differences in the two papillae. The dorsal papilla is surmounted by a tectorial membrane that makes contact with a fiber plate lying over the middle hair cells, whereas the ventral papilla exhibits no tectorial membrane connections but bears a row of sallets resting on the tufts of the hair cells.

This study of the lacertid ear has now been extended to another species, *Eremias argus* (Peters, 1869).† Two living specimens were obtained and, after measurements of the sensitivity of their ears had been carried out in terms of cochlear potentials, the ear tissues were prepared for histological study.

Materials and Methods.—Cochlear potential measurements: To record cochlear potentials in response to tonal stimuli, the animal was deeply anesthetized with ethyl carbamate, and the pharyngeal region on the right side was exposed by a longitudinal incision through the floor of the throat. A small silver bead electrode was placed on the round window membrane, a second bead electrode was placed on inactive tissues in the region of the incision, and a third (grounded) electrode in the form of a stainless steel needle was inserted beneath the skin of the throat. These electrodes led to the three input terminals of a balanced preamplifier, which provided about 80 db rejection of stray potentials, such as those from power lines, that might be picked up by the electrodes. The preamplifier produced a gain of 1000 times, and its output was led to a wave analyzer used as a selective voltmeter. Cochlear potentials as small as 0.03–0.04 microvolts (rms) were measurable for all but the lowest tones, the noise level for which was most disturbing. For these tones, the measurements were taken at higher levels up to 0.1 μv. Experience has shown that cochlear potential measurements in the lizard ear are best carried out at as low a level as possible, within the limit imposed by noise, because when exposed to strong sounds this ear becomes unstable and nonlinear and is particularly susceptible to damage.

Results.—Figure 1 shows sensitivity curves for the right ears of two specimens in terms of the sound pressure (in decibels relative to 1 dyne/cm^2) required to produce a standard response of 0.1 μv. The sound pressure needed for 0.1 μv was calculated for the tones for which measurements were made at smaller response levels; this calculation is valid within the range of linearity of the response.

The results for the two specimens are in good agreement for the low tones and agree fairly well for the high tones, but they differ somewhat in the middle range. Both curves show two regions of best sensitivity, 600–700 and 2500–3500 cps. In general, the sensitivity is poor compared with the large majority of lizard ears. However, the ear of *Eremias argus* is more sensitive than that of the lacertid *Eremias velox persica* previously studied;[6] the former registered from 20 to 30 db greater sensitivity.

Anatomical observations: The ears were prepared for histological study by the method described previously,[7] which included fixation by perfusion through the circulatory system, embedding in celloidin, and special staining to bring out the inner ear structures, especially the hair cells. Sections were cut at 20-μ intervals through the region of the ear, and all sections were mounted to form a complete series.

From photomicrographs of the sections through the ear region, a scale model

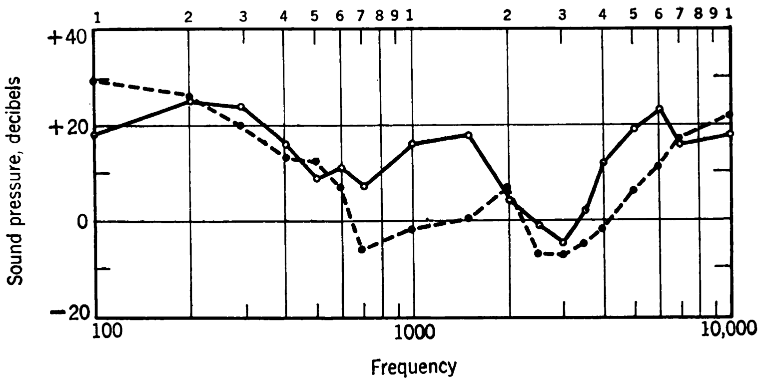

FIG. 1.—Sensitivity curves for two specimens of *Eremias argus.* Sound pressure, in decibels relative to 1 dyne/cm^2, required to produce a cochlear potential of 0.1 μv.

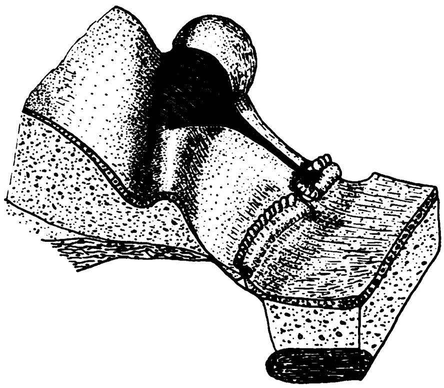

FIG. 2.—Reconstruction of the right ear of *Eremias argus*, as seen from behind and somewhat above and laterally.

was constructed that served as the basis for Figure 2. This sketch is of the right ear drawn from behind and somewhat above and laterally.

Shown are medial and lateral portions of the limbic plate and, between them, the two papillae resting on (and largely obscuring) the two basilar membranes. The medial portion of the limbus shows a prominent thickening which forms a crest that is rather high in the dorsal region (reaching 134 μ at one point) and rapidly becomes lower toward the ventral end.

Arising from the dorsomedial region of the limbic crest is the tectorial membrane, which is rather broad at its origin but tapers rapidly and leaves the crest as a narrow ribbon. It is extended to the dorsal papilla, and its lateral end is attached to a fiber plate that rests upon the hair tufts of the more ventral hair cells. The more dorsal hair cells of this papilla bear fiber plates or sallet-like bodies, and have no obvious connections to the tectorial membrane.

The ventral papilla is about half again as long as the dorsal papilla, and has no tectorial membrane connections. Along this papilla, lying on the tips of the hair tufts, is a single line of sallets, which are in close contact with one another and grow progressively smaller in the ventral direction. As this papilla proceeds ventrally it undergoes a peculiar twist and, along with its sallets, it changes from an upright position to a nearly horizontal position, as shown.

Further details of this structure and the variations along its extent are best seen in a series of drawings that represents selected sections through a particular ear.

Figure 3 shows a section through the dorsal papilla at a point about 80 μ from the dorsal end of its basilar membrane. The limbic crest is still high (measured in one specimen as 119 μ), but no tectorial membrane is present. Resting on the hair tufts is a sallet with a broad conical shape. The papilla is borne by a rather thick fundus.

Figure 4 shows a section 30 μ farther along, which still passes through the dorsal papilla. The limbic crest is not as high as before, and it bears on its medial side a tectorial membrane that seems to begin at the sharp rise of the crest. This membrane adheres closely at the elevation of the crest, and then comes free as the crest falls sharply away. It extends over the papilla and is attached to the flat fiber plate. Here the papilla contains four rows of hair cells, and the fundus has become rather thin.

Figure 5 shows a section through the isthmus between the two basilar membranes. The location is 220 μ from the dorsal end of the dorsal membrane. The tissue here is the same in character as elsewhere in the limbus, and the epithelial cells form a continuous covering. The limbic crest is still lower than before.

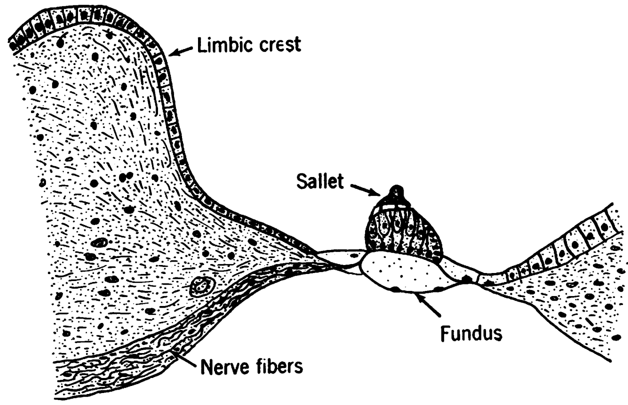

FIG. 3.—A transverse section through the dorsal part of the dorsal papilla at a point 80 μ from the dorsal end.

The tectorial membrane can still be seen, but it extends only a short distance beyond the limbic crest.

Figure 6 shows a section through the initial (i.e., dorsal) portion of the ventral papilla at a point 60 μ from the preceding section, or 280 μ from the dorsal end. The limbic crest is lower still, and the tectorial membrane is seen only on the rounded elevation of the crest. The papilla rests on a rather thick fundus. It contains two rows of hair cells and bears a sallet of a tall columnar shape.

Figure 7 shows a section through the more ventral part of the ventral papilla, 140 μ from that shown in Figure 6. The limbic crest is rather low, and there is no trace of a tectorial membrane. The papilla contains three rows of hair cells and is turned so that the long axes of these cells are nearly parallel to the basilar membrane. The papilla seems precariously poised on the edge of a triangular fundus, weakly anchored by the border cells. The sallet is small and is inclined medially, as is the papilla.

Some quantitative details of structure are presented in Figure 8. In (*a*) of this figure are charted the varying widths of the two basilar membranes along a

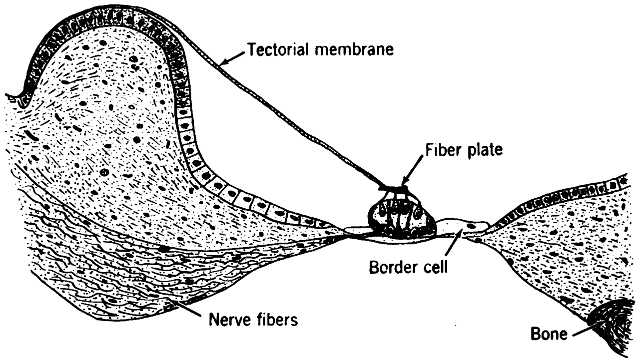

FIG. 4.—A section through the ventral part of the dorsal papilla at a point 110 μ from the dorsal end.

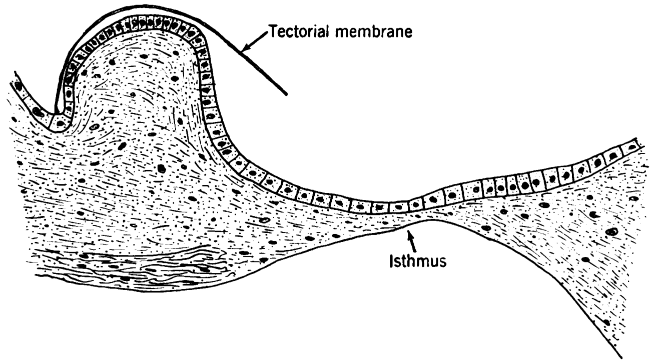

FIG. 5.—A section through the isthmus between dorsal and ventral papillae. The position is 220 μ from the dorsal end of the dorsal papilla.

scale that begins at the dorsal end of the dorsal basilar membrane and extends to the ventral end of the ventral basilar membrane, a distance of 500 μ. The dorsal basilar membrane is 180 μ long and the ventral one is 265 μ long, a ratio of about 2:3. The dorsal membrane is the broader and reaches a width of 100 μ at a point about two thirds of its length, after which it narrows rapidly. The ventral membrane rapidly increases in width to a maximum of 80 μ, after which it slowly narrows to 60 μ and ends bluntly.

Among the four ears studied, the width of the isthmus separating the two basilar membranes varied. In the ear described above, it was 40 μ, and in the others it varied from 60 to 80 μ.

The fundus in each papilla (see Fig. 8*b*) has much the same form as its basilar membrane but is only about half as wide. In the dorsal papilla it increases sharply in thickness from the dorsal end, attains a maximum of 28 μ, and then rapidly narrows (Fig. 8*c*). In the ventral papilla, the fundus likewise thickens rapidly, reaches a maximum of 23 μ, and then, after some irregularity, declines to its ventral end.

The cross-sectional area of the two papillae is represented in Figure 8*d* by the

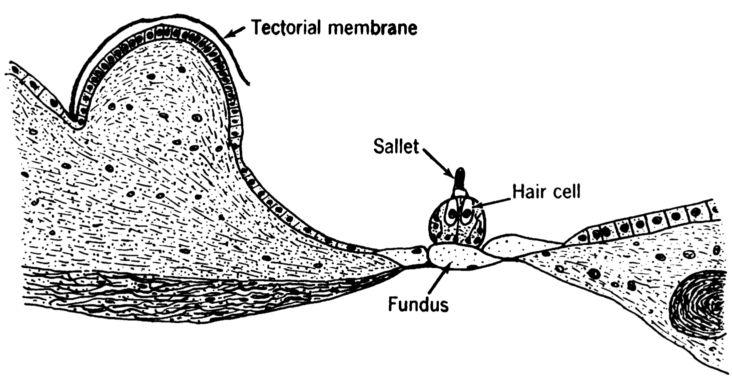

FIG. 6.—A section through the dorsal part of the ventral papilla. The position is 280 μ from the dorsal end of the dorsal papilla.

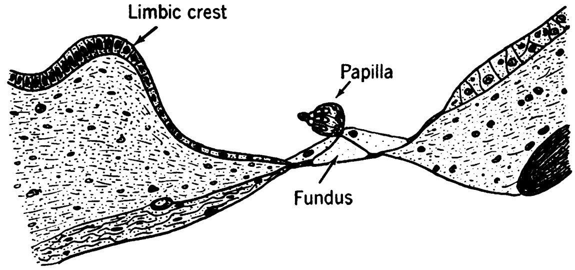

FIG. 7.—A section through the ventral part of the ventral papilla. The position is 420 μ from the dorsal end of the dorsal papilla.

solid lines, and the area of the organ of Corti (i.e., all except the fundus) is shown by the broken lines. In the dorsal papilla, the form is rather symmetrical, with a flat maximum reached just dorsal of the midregion. In the ventral papilla, the form is markedly asymmetrical, with the maximum appearing near the dorsal end and falling off progressively to the ventral end.

The number of rows of hair cells as seen in a transverse section is charted in Figure 8*e*. In the dorsal papilla, there are three rows at the dorsal end, then six, then the number decreases progressively to three rows at the ventral end. The number of rows at the ventral end is first two, then four in one section, then three, and finally two rows appear over the ventralmost portion of the papilla.

There are 51 hair cells in each papilla of the ear described above, a total of 102 for both papillae. In the other ear of the same specimen, there were 47 in the dorsal papilla and 48 in the ventral papilla, for a total of 95.

Discussion.—The structural picture presented here is closely similar to that already described for *Eremias velox persica*,[5] but a number of additional details have been brought out in the present study. The significance of many features of this ear is a matter for speculation.

It is probable that the hair cells belonging to the two papillae are stimulated in different ways when their basilar membranes are caused to vibrate under the influence of sound. The tufts of the hair cells of the dorsal papilla that have tectorial membrane connections would be subject to restraint, so that when the cell bodies are moved up and down, the tufts would remain relatively fixed. Hence, there would be relative motion between the cilia and bodies of these cells, with resulting stimulation. The tufts of the hair cells of the ventral papilla incur no such restraint, but they are in intimate contact with an overlying sallet. The sallet appears to be constituted of a very dense tissue, and hence it would have inertia. Thus, when the basilar membrane moved in response to sound, the sallet would move to a lesser extent and would lag behind. Again, there would be relative motion between the body of the hair cell and the tips of its cilia, to produce stimulation. However, this stimulation, with a given sound, may be expected to be smaller and to vary in phase from that produced in the hair cells that have tectorial membrane connections.

There are hair cells in the dorsal papilla (Fig. 3) that are served by sallets and have no tectorial membrane connections, or at least no direct ones. It is possible that these cells have indirect connections (somewhat analogous to those attributed to iguanids[5]) because they seem to form a tight chain that is in contact with the fiber plate to which the tectorial membrane is attached and thus they incur

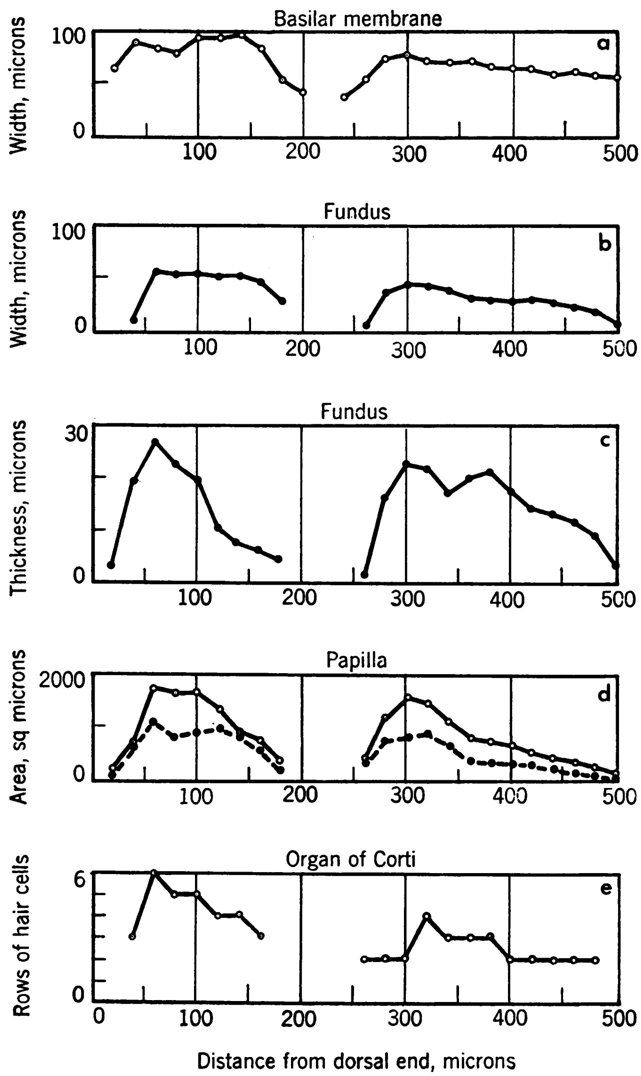

FIG. 8.

a measure of restraint in their motions. Another possibility is that these cells operate in just the same manner as the cells of the ventral papilla and are stimulated through the inertia of their sallets. There is, finally, the possibility that the principles of restraint and inertia both operate for these hair cells, in which case their stimulation can be expected to have intensity and phase relations intermediate between those of the two principal types of hair cells.

Summary.—An unusual feature of lizards of the family Lacertidae is the presence in each ear of two separate basilar membranes. A study of the lacertid *Eremias argus* (Peters) shows that the auditory papillae borne by the two basilar membranes are significantly different in structure. In one (the dorsal papilla)

certain hair cells have connections with a tectorial membrane. In the other (the ventral papilla) there are no such connections. Instead, these hair cells are provided with sallets that rest upon the cilia.

It is suggested that there is a difference in the mode of action of sound vibrations on the hair cells with tectorial membrane connections and on those bearing sallets: for those of the first (tectorial) type, a principle of restraint operates so as to produce a relative motion that causes stimulation, and for those of the second (sallet) type, a principle of inertia operates to give an effect that is likewise stimulatory but differs in its effectiveness and in its phase relations.

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† For confirmation of species identification, I am indebted to Dr. Clarence J. McCoy, Jr., of the Carnegie Museum, Pittsburgh. The bodies of the specimens have been deposited and classified in the museum as CM47561 and CM47562.

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